贵州关岭晚三叠世一大型鱼龙类头骨1)

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摘要 记述了产自贵州关岭上三叠统杯椎鱼龙属一新种——亚洲杯椎鱼龙(Cymbospondylus asiaticus sp. nov)。标本为两件几乎完整的头骨,产于法朗组瓦窑段的泥质灰岩中,这是目前已知惟一的晚三叠世 Cymbospondylus 属的标本,也是该属时代最晚的一个种。亚洲杯椎鱼龙头部最明显的特征是下颌牙齿仅分布于齿骨的前半部分。此外,新种的吻部极长,超过头骨全长之半,上颌骨非常发达,并且具有已知鱼龙类中最小的眼眶。亚洲杯椎鱼龙是这一大型鱼龙类在北美和欧洲以外地区的首次记录。

关键词 贵州关岭,晚三叠世,法郎组,鱼龙类

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Cymbospondylus 属是 Leidy(1868)根据产自北美 Nevada 山脉中三叠统的一批材料建立的,当时共有 3 个种, C. petrinus、C. grandis 和 C. piscosus。Merriam(1908)详细描述了产于同一地点保存完好的 C. petrinus。此后,陆续有一些该属的新种发表,标本产地除北美外还有欧洲。但是除 C. petrinus 和 C. parvus 以外,各个种的有效性都颇多争议(Merriam,1908; Huene,1916; Broili,1916)。Sander(1989)建立并描述的 C. buscheri 是瑞士中三叠世Monte San Giorgio 动物群的标本,化石材料是继 1908 年 Merriam 描述的 C. petrinus 标本之后第二个比较完整的个体,产于 Anisian-Ladinian 界限上。到目前为止,Cymbospondylus 属的完整标本极少,全部产于北美及欧洲的中三叠世地层。这一属的鱼龙都是一些体形较大的种类,在大洋间游泳迁移的能力很强,具有广泛的地理分布,关岭地区发现的标本进一步将其古地理分布扩展至东特提斯洋区。由于法郎组瓦窑段的地层年代为晚三叠世卡尼中期(杨守仁等,1995),C. asiaticus 成为该属目前已知的最晚代表。

鱼龙目 Ichthyosauria Blainville, 1835 萨斯特鱼龙科 Shastasauridae Merriam, 1902 杯椎鱼龙属 Cymbospondylus Leidy, 1868 亚洲杯椎鱼龙(新种) Cymbospondylus asiaticus sp. nov.

正型标本 一件基本完整的头骨及下颌,立体保存,全长 106cm,几乎无变形,惟头骨枕面缺失,下颌前方略有破损。中国科学院古脊椎动物与古人类研究所标本编号:IVPP V 11865(图 1)。

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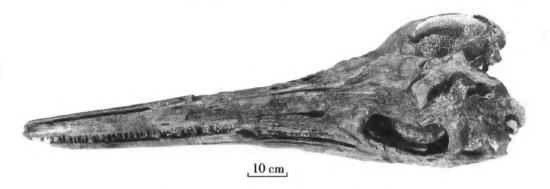


图 1 亚洲杯椎鱼龙(新种)正型标本 V 11865 Fig.1 Cymbospondylus asiaticus sp. nov., Holotype V 11865

副型标本 一件侧向挤压的头骨,长 85cm, 吻端略有缺失。中国科学院古脊椎动物与古人类研究所标本编号;IVPP V 11869(图 2)。

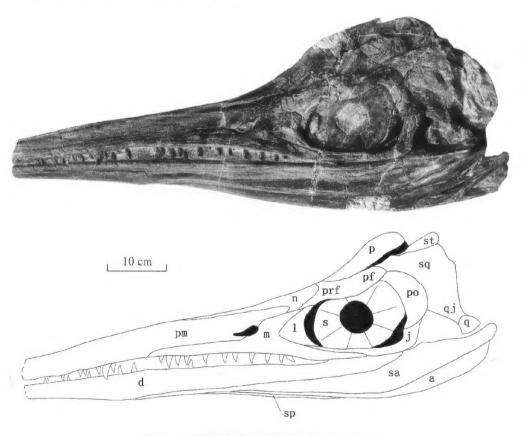


图 2 亚洲杯椎鱼龙(新种)副型标本 V 11869

Fig. 2 Cymbospondylus asiaticus sp. nov., Paratype V 11869

简字说明 Abbreviations: a, angular 隅骨;d, dentary 齿骨;j, jugal 轭骨;l, lacrimal 泪骨;m, maxilla 上颌骨;n, nasal 鼻骨;p, parietal 顶骨;pf, postfrontal 后额骨;pm, premaxilla 前上颌骨;po, postorbital 眶后骨;prf, prefrontal 前额骨;q, quadrate 方骨;qj, quadratojugal 方轭骨;s, sclerotic bone 巩

膜骨;sa, surangular 上隅骨;sp, splenial 夹板骨;sq, squamosal 鳞骨;st, supratemporal 上颞骨

特征 外鼻孔由极为发达的上颌骨与前上颌骨围成。吻部长度占头骨长度的比例大(约为头骨全长的54%)。眼眶前后径就与头骨长度的比例而言很小。泪骨呈三角形,鼻骨与鳞骨不接触。额骨不进入颗孔。上颌前部牙齿着生在完整的齿窝内,下颌的牙齿只分布于齿骨的前半部分。

词源 asiaticus,拉丁词,意为亚洲的。

产地与层位 贵州省关岭县新铺乡;上三叠统,法郎组瓦窑段。

描述 中到大型的鱼龙类。前上颌骨狭长,后部呈凹陷状,外鼻孔背侧的一支比腹侧 的一支长,并延伸至鼻孔之后。上颌骨非常发达,前端达到前上颌骨中部,后端超越眼眶 前缘之后,达到眼眶中部。上颌骨的上升支粗壮,插入泪骨与前上颌骨、鼻骨之间,最上端 与前额骨接触。外鼻孔狭长,呈犁形,前窄后宽,基本上位于头骨的背侧,由前上颌骨与上 颌骨围成。泪骨非常发达,大致呈三角形。鼻骨前部极为狭长,尖灭于两前上颌骨之间, 后端远远位于外鼻孔之后。由于前上颌骨末端向后延伸,鼻骨被排除于外鼻孔之外。眼 眶呈椭圆形,就与头骨比例(约占头骨全长的15%)而言,眼眶的大小显然不及周氏黔鱼 龙(32%)(李淳,1999)。巩膜环保存极为完整,在副型标本上约由7~9枚巩膜骨环绕而 成。巩膜环外径 13.5cm,内径 5.3cm。额骨相对较小,长度远远短于鼻骨,其最宽处位于 与顶骨的交界处。前额骨与后额骨组成眼眶的上缘,二者的接缝不清晰。标本右侧颞孔 周围的骨骼保存不佳,仅从左侧判断,后额骨似乎并未进入颞孔。颞孔长度为头骨全长的 12%~14%,其周边骨片为顶骨、鳞骨及上颞骨(supratemporal bone)。顶骨具发达的矢状 眷和人字眷。顶孔很小,位于矢状眷前缘,完全处于顶骨内部。眶后骨位于后额骨与鳞骨 之下,构成眼眶的后缘。颊部(包括眶后骨、鳞骨和方轭骨)占头骨全长的10.3%,在周氏 黔鱼龙这个比例是8.9%。上颞骨发达,位于颞孔的后端。方轭骨由于破损与鳞骨的接 缝观察不到。C. asiaticus 上颌的牙齿为槽生齿或亚槽生齿,齿列为单列,与晚期鱼龙类 相比牙齿排列不紧密。牙齿呈圆锥状,表面具纵纹,尖端略向后弯。最前面的两枚牙齿明 显向后倾倒。副型标本的货列相对较完整,显示该个体生活时正经历牙货替换,货列中的 牙齿大小不一,有些显然才萌生不久,另有许多齿虚位,仅有空的齿槽。副型标本上可观 察到的上颌牙齿有 14 枚(左侧),而齿位约为 60 左右。头骨的各项主要测量数据见表 1。

表 1 亚洲杯椎鱼龙(新种)标本测量

Table 1 Measurements of the skull of C. asiaticus sp. nov. (cm)	
头骨全长 total length	106
吻端至鼻孔前缘 from rostrum to anterior margin of nares	56.8
吻端至眼眶前缘 from rostrum to anterior margin of orbit	70
眼眶长 length of orbit	16,左 left; 17,右 right
颗孔长 length of temporal fenestra	13.左 left,15.右 right
類部长 length of cheek region	11
头骨最大宽 maximal width of cranium	31
鼻孔间隔宽 width between naries	7.5
巩膜环外径(副型标本) outer diameter of the scleral ring in paratype	15
巩膜环内径(副型标本) inner diameter of the scleral ring in paratype	5.5
顶孔长 length of the parietal foreman	1.7
顶孔宽 maximal width of the parietal foreman	1

下颌的结构在鱼龙类的各属种中没有实质性差别,各种骨骼成分都存在,并且极度拉长。冠状骨在鱼龙类的报道中较少涉及,该骨片即使存在也应该很小(Romer,1956)。副型标本显示 C. asiaticus 的冠状骨是存在的,而且形成了一个不十分发达的冠状突。上隅

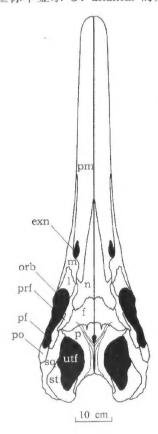


图 3 亚洲杯椎鱼龙(新种) 头骨复原

Fig. 3 Reconstruction of Cymbospondylus asiaticus sp. nov. 简字说明 Abbreviations: exn, external naris 外鼻孔;f, frontal 额骨; l, lacrimal 泪骨; m, maxilla 上颌骨;n, nasal 鼻骨; orb, orbit 眼眶;p, parietal 顶骨; pf, postfrontal 后额骨; pm, premaxilla 前上颌骨; po, postorbital 眶后骨;prf, prefrontal 前额骨; sq, squamosal 鳞骨; st, supratemporal 上颞骨; utf, upper temporal fossa 上颞窝

骨的上缘在鱼龙类往往形成一个类似冠状突的小突起,这一结构在 C. asiaticus 的下颌上也十分明显。 C. asiaticus 下颌的最特别之处在于其齿列,这些具纵纹的锥状牙齿只着生于下颌的前半部分。下颌后部不仅观察不到牙齿,也没有牙齿萌生的齿槽。换言之,上颌后半部分的牙齿在下颌的相应位置上没有与之咬合的对象。

头骨腭面可以辨认出 4 种骨骼成分,即腭骨、翼骨、副蝶骨和上颌骨,都十分狭长。由于缺少外翼骨,鱼龙类中由腭骨、翼骨、方骨、轭骨以及上颌骨所围成的孔被解释为从双孔类(diapsida)祖先中继承下来的下颞孔(subtemporal opening)及眶下孔(suborbital opening)的复合体(Callaway,1989)。这个狭长的开孔在我们的标本上由于下颌的挤压而观察不到。内鼻孔主要开在腭骨上,前缘有部分犁骨和上颌骨成分。

比较和讨论 尽管头后骨骼没有保存,但将这两件大型 的鱼龙类头骨置于 Cymbospondylus 属是合适的(图 3)。除了 具有晚期鱼龙类的一些特征外,它清晰地表现出 Cymbospondylus 属头部的典型特征组合:吻部窄而狭长,几乎完全由前 上颌骨构成;上颌骨极大;眼眶相对较小,呈椭圆形;鼻孔周 边仅为前上颌骨与上颌骨,无其他骨骼成分;牙齿着生于齿 窝中。另外 C. asiaticus 隅骨后部与上隅骨的最大宽度之比 也与 Cymbospondylus 的几个已知种最为接近(Motani, 1999)。 Cymbospondylus 的眼眶就比例而言是鱼龙类中最小的,而 C. asiaticus 眼眶的相对长度在该属中又最小:眼眶与头骨全长 之比在 C. asiaticus 中为 15.09%, 在 C. petrinus 中为 16.15% (据 Merriam 1908 图版)。Sander(1989)描述 C. buchseri 时给出其眼眶长与眶后部分长之比为 1.7,该比值在 C. asiaticus 中为 1.39。C. asiaticus 吻部所占的比例也较 C. pterinus 为大,达到了头骨全长的 54 %。在副型标本上可以辨 别出 C. asiaticus 的巩膜环由 7~9 枚巩膜骨组成,少于Sander (1989)描述 C. buchseri 时记录的 13 枚和 Merriam (1908)在 C. pterinus 中记录到的 16 至 18 枚。C. asiaticus 的下颌齿列 仅分布于齿骨的前部,这种现象在其他鱼龙类中尚无记录, 是亚洲杯椎鱼龙最明显的特征之一。

董枝明(1972)描述的西藏喜马拉雅鱼龙(Himalayasaurus 骨; st, supratemporal 上颞骨; tibetensis)是我国另一种大型的晚三叠世鱼龙。该材料比较破utf, upper temporal fossa 上颞窗 碎,可供对比的部分仅为牙齿。喜马拉雅鱼龙的牙齿着生于

开放的齿沟中,与 C. asiaticus 的槽生齿或亚槽生齿区别十分明显。尹恭正等(2000)记述并命名的两种大型鱼龙类,邓氏贵州鱼龙(Guizhouiethyosaurus tangae)和蔡胡氏典型鱼龙(Typicusichthyosaurus tsaihuae)也是产于关岭地区的标本。仅从图版观察¹¹,这两件标本非常相似,只是保存的角度不同。文中涉及的头骨性状多为测量数据,故无法与之进行实质性的对比。

鱼龙类牙齿的着生方式是一个非常复杂的问题, Motani(1997)对有关术语进行了规范并对鱼龙类予以总结。尽管如此,各类牙齿着生方式间的界线仍不十分清晰。 C. asiaticus 的副型标本由于受到挤压而极度侧扁,但上颌前半部的牙齿似乎是比较标准的槽生齿,因为在一些牙齿脱落的齿位上可以见到四壁完整的齿槽。上颌后部牙齿基部的内侧是暴露的,此种情形在目前只能判断为亚槽生或侧生,根据其总体形态与蜥蜴类典型的侧生齿相比,将其定性为亚槽生更为合适。下颌齿列的前后部分都可以观察到完整的齿槽,但是目前还不能否定有亚槽生齿的存在。除了 Cymbospondylus 属外,上述情况还与晚三叠世的 Shonisaurus popularis (Camp, 1980; Motani, 1997)比较接近。

鱼龙类外鼻孔周边的骨骼通常为前上颌骨、上颌骨、鼻骨和泪骨。但是某些属种中往往较少,比如在早三叠世的 Grippia 和中三叠世的 Mixosaurus 两属中,泪骨由于上颌骨上升支的插入而与外鼻孔分隔,在中三叠世的 Cymbospondylus 中,鼻骨由于前上颌骨末端的延长而与外鼻孔相分离,另外泪骨即使参与外鼻孔的组成,所占比例也极小(Romer, 1956; Massare and Callaway, 1990; Motani, 1999)。而早侏罗世进步的 Ichthyosaurus 中,上颌骨缩小,从而被排除于鼻孔周边之外。因此,外鼻孔周边的骨骼成分,除 Cymbospondylus 可能为两枚外,在上述其余几个属中均由三块骨片组成。

到目前为止,从动物群的角度看,贵州全境内的三叠纪海生爬行动物化石同时具有西特提斯动物群和东太平洋动物群的特征,关岭动物群中的海龙类(Rieppel et al., 2000; Liu and Rieppel, 2001)及鱼龙类(李淳,1999; 尹恭正等,2000)在现今的欧洲和北美都有类似化石出现。这种现象与该地区在三叠纪时所处的古地理位置,即处于这两个动物群之间是相符合的。 Cymbospondylus 是游泳能力很强的大型鱼龙类,此次在我国西南地区发现这类动物的化石,进一步说明了它们具有近乎全球性的广泛分布,同时将这个属的时代分布从中三叠世延伸到了晚三叠世。 楯齿龙类长期以来只发现于欧洲、中东和北非部分地区,2000 年在关岭发现的豆齿龙类首次将这类动物的化石扩展至西特提斯洋以外区域(李淳,2000; 尹恭正等,2000)。 在北美地区找到楯齿龙类化石之前,这种游泳能力显然较弱的近岸海生爬行动物似乎表明我国南方与西特提斯洋在古动物地理方面的关系更近一些。关岭邻近地区发现的三叠纪鱼类化石同样表明这种密切的动物地理关系(苏德造,1959; 金帆,2001)。

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^{1) 2000} 年笔者赴贵阳时这批标本仍掌握在私人收藏者手中,笔者未获许观察标本。

CYMBOSPONDYLUS FROM THE UPPER TRIASSIC OF GUIZHOU, CHINA

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Abstrect A new species of *Cymbospondylus* is named and described on the basis of two well-preserved skulls from the Late Triassic Wayao Member of the Falang Formation at Guanling, Guizhou Province. The prominent character of the new species is the teeth on the lower jaw, which only exist on anterior half of the dentary. Furthermore, it has large maxilla and relatively, has the smallest orbit in the known ichthyosaurs. This is the latest occurrence of the genus *Cymbospondylus*, which is previously known only from the Middle Triassic of North America and Europe.

Key words Guanling, Guizhou, Late Triassic, ichthyosaurs

The genus Cymbospondylus was erected by Leidy (1868), who described three species. C. petrinus, C. grandis and C. piscosus, based on fragmentary material from Middle Triassic rock of Nevada. Merriam (1908) gave an exhaustive description of C. petrinus based on an excellently preserved specimen from the same locality. From then on, several species that came from North America and Europe were erected, but the validity of these species is doubtful, except for C. petrinus and C. parrus (Merriam, 1908; Huene, 1916; Broili, 1916). C. buscheri (Sander, 1989), which is found from Anisian-Ladiaian boundary of Middle Triassic in Monte San Giorgio, Switzerland, is the second best known member of the genus. Hence, by far all materials of Cymbospondylus are known from the Middle Triassic of North America and Europe. Here we report a new species of this genus that was collected from the Late Triassic in southeastern China.

Order Ichthyosauria Blainville, 1835
Family Shastasauridae Merriam, 1902
Cymbospondylus Leidy, 1868
Cymbospondylus asiaticus sp. nov.

(Fig.1~2)

Diagnosis Large-sized Cymbospondylus. The external naris bordered by large maxilla and premaxilla. Differs from C. pterinus and C. buchseri in having relatively long rostrum (54 % total length of the skull), very small orbit, triangular lacrimal and no contact between the nasal and squamosal. Dentary teeth distributed over the anterior half of the lower jaw.

Holotype A nearly complete skull preserved in three-dimensions, with the occipital part and the most anterior rostrum missing. V 11865(Fig.1).

Paratype A nearly complete skull. V 11869(Fig.2).

Type locality and horizon Guanling County, Guizhou Province, China; Late Triassic.

Etymology The species name is derived from Latin and, refers to "Asia".

Description and comparison The premaxilla is significantly elongated and extends posteriorly beyond the naris. Its posterior end is concave with the dorsal process much longer than the ventral

process. The external naris is an elongate slit, caudodorsally orientated and bounded by the premaxilla and the maxilla. The maxilla is relatively large, more than 1/3 the length of the premaxilla. The ascending process of the maxilla is strong and excludes the lacrimal, which is triangular in shape and forms the anterior margin of the orbit, from the border of the external naris. The nasals are well developed, long and slender. They taper anteriorly, wedging into the beak between the premaxillae, and their posterior ends terminate far beyond the naris. The nasals are also excluded from the external naris by the caudal projections of both the premaxilla and the maxilla. The jugal, which is very slender, forms the ventral border of the orbit, and is overlapped caudally by the postorbital, although the suture can not be clearly determined. The orbit is oval and dorsoventrally compressed. the ratio of its length to the postorbital length of the skull is 139 %. The sclerotic plate is nearly perfectly preserved. In the paratype, about 7 ~ 9 sclerotic bones can be distinguished, much fewer than that in C. buchseri (Sander, 1989). In the holotype, these plates curve backward around a considerable segment of the eyeball and the sclerotic ring lean to the posterior half of the orbit, while in the paratype, it is in the middle of it. The postorbital is lune shaped and forms the posterior margin of the orbit. As in C. buchseri (Sander, 1989), it exhibits a narrow contact with the postfrontal rostrally; posteriorly it contacts the squamosal more extensively. The frontal is relatively small, obviously shorter than the nasal, with its widest position along the frontal-parietal suture. The prefrontal appears larger than that of C. buchseri, and contributes about half to the rostrodorsal margin of the orbit. The suture between the prefrontal and the postfrontal is difficult to determine. Similar to that in C. buchseri, there is a very narrow contact between the prefrontal and the squamosal, but there is no contact between the nasal and the squamosal. The rostral process of the squamosal contributes about 25 % to the upper temporal fenestra. The parietals are strongly crested as in some derived genera of ichthyosaurs, with a very small parietal foramen entirely within. The supratemporal bone is well developed. The temporal fossa is relatively small, bordered by the parietal, squamosal, and the supratemporal. It seems that neither the postorbital nor the postfrontal contributes to the border of temporal fossa. The cheek is relatively wide. The suture between the quadrate and the quadratojugal can not be distinguished due to the poor preservation of this region. The teeth are sharppointed, with longitudinal grooves on its surface; the total number is about 60. The measurements of the skull elements are given in Table 1.

The lower jaw is long and slender. The coronoid forms a small coronoid process. Another small process exists behind it, which is formed by the thickened surangular. The lateral exposure of the angular is smaller than that of the surangular. It is interesting to note that the dentition only exists on the anterior half of the mandible.

The teeth on the anterior upper jaw seem to be typical thecodont, as shown by the complete sockets left by the teeth. However, the teeth on the posterior half of the upper jaw are probably subthecodont as described by Motani (1997).

In ventral view the maxilla, palatine, pterygoid and parasphenoid are all greatly elongated. Ichthyosaurs lack ectpterygoids, so the single large, elongate opening on each side is usually interpreted as a contiguous suborbital and subtemporal opening resulting from the reduction and loss of ectpterygoid (Callaway, 1989). This opening can not be seen in our material for the extrusion of the lower jaw. The inner naris is bordered mostly by the palatine, and partly by the maxilla and the vomer.

Discussion Although no post-cranial skeleton is preserved, there seems to exist sufficient evidence to refer the described material to *Cymbospondylus* (Fig. 3). For instance, the rostrum is long and slender and mainly formed by the premaxilla; the maxilla is large; the naries are only bordered by the premaxilla and maxilla. Furthermore, the new material has a relatively small depressed oval orbit. It is even smaller than that of *Cymbospondylus*, which was believed to have the smallest orbit before. The ratio between the orbit length and cranial length in *C. asiaticus* is 15.09 %, and in *C. petrinus* it is about 16.15 % (based on the plates of Merriam, 1908). Sander (1989) reported

a ratio of 170 % between the orbit length and the postorbital length of the skull in C. buchseri, in C. asiaticus it is 139 %. The rostrum, which consists largely of the premaxillae, is relatively longer than that of C. pterinus, reaching 54 % the total length of the skull. The sclerotic plate is nearly perfectly preserved. In the paratype, there are about $7 \sim 9$ sclerotic bones can be distinguished, much fewer than 13 in C. buchseri (Sander, 1989) and $16 \sim 18$ in C. petrinus (Merriam, 1908). The most striking features of the skull is the teeth on lower jaw, which are only implanted on the anterior part of the mandible.

Himalayasaurus tibetensis is another large late Triassic ichthyosaur discovered in China (Dong, 1972). The specimen is poorly preserved and only the teeth are comparable to our material. The tooth of Himalayasaurus tibetensis is implanted in the open groove of mandible, quite different from that of C, asiaticus, which is placed in a separate pit.

Montani (1997) gave a general discussion on tooth implantation and replacement in ichthyosaurs. According to his terminology, the tooth implantation of *C. asiaticus* could be defined as "ichthyosaurian thecodont type", similar to that of other *Cymbospondylus* and *Shonisaurus*.

By far the Triassic marine reptile fauna in Guizhou Province shows the characters of both western Tethyan Fauna and the eastern Pacific Fauna. This dual affinity is congruent with the paleobiographical position of southeastern China. The ichthyosaurs (Li. 1999; Vin et al., 2000) and thalattosaurs (Rieppel et al., 2000; Liu and Rieppel, 2001) from Guanling area are also known from the Triassic deposits of Europe and North America. *Sinocyamodus xinpuensis* (Li. 2000) is the first placodont discovered outside western Tethyan region. This near-shore poor swimmer supports a close relationship between Guanling Fauna and the western Tethyan Fauna. This relationship is also supported by the fossil fishes discovered in adjacent areas (Su, 1959; Jin. 2001).

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